Potato Germplasm Collecting Expedition to Mexico in 1997: Taxonomy and New Germplasm Resources

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ABSTRACT

Wild potato (*Solanum* sect. *Petota*) germplasm has been collected in Mexico on nine major expeditions, as determined by 20 collections or more from each expedition currently at the United States potato genebank, the National Research Support Program-6 (NRSP-6). These have resulted in 609 accessions with good collection data. In addition, NRSP-6 has germplasm of approximately 90 other Mexican collections that are unspecific regarding date or place of collection. This expedition was funded to collect those remaining collections with no or little germplasm: *Solanum clarum*, *S.* x *edinense*, *S. hintonii*, *S. hjertingii* var. *physaloides*, *S. leptosepalum*, *S. lesteri*, *S. macropilosum*, *S.* x *michoacanum*, *S.* x *sambucinum*, and *S. stenophyllidium*. In addition, some species and species groups (species groups indicated in parentheses) have unresolved taxonomic problems that needed clarification by additional field collections. These are (*S. agrimonifolium* and *S. oxycarpum*), (*S. brachycarpum*, *S. guerreroense*, *S. hougasii*, and *S. iopetalum* - the *S. brachycarpum* complex), (*S. fendleri*, *S. papita*, *S. stoloniferum* - the *S. stoloniferum* complex), *S. leptosepalum*, and *S. macropilosum*. We conducted a wild potato germplasm collecting expedition in Mexico from August 22 to October 31, 1997. Our 103 collections, 71 as germplasm collections, provide the first germplasm samples for *S. hjertingii* var. *physaloides*, *S. leptosepalum*, and *S. macropilosum*. They provide additional germplasm of the rare species *S. clarum*, *S.* x *edinense*, *S. lesteri*, *S.* x *michoacanum*, *S.* x *sambucinum*, and *S. stenophyllidium*. We additionally gathered germplasm and field data to help resolve taxonomic difficulties in *S. agrimonifolium* and *S. oxycarpum*, the *S. brachycarpum* complex, and the *S. stoloniferum* complex.

INTRODUCTION

Solanum L. sect. *Petota* Dumort., the potato and its relatives, occurs from the southwestern United States to south-

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ADDITIONAL KEY WORDS: *Solanum* sect. *Petota*.

EXPLANATION OF ABBREVIATIONS
CHAP, Herbario, División de Ciencias Forestales, Universidad Autónoma Chapingo, Chapingo, Edo. de México, Mexico
CHAPA, Herbario-Hortorio, Centro de Botánica, Colegio Postgraduados, Chapingo, Edo. de México, Mexico
ENCB, Departamento de Botánica Herbarium, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico City, Mexico
F, Field Museum of Natural History Herbarium, Chicago, IL, USA
GH, Gray Herbarium, Harvard University, Boston, MA, USA
IEB, Herbario, Centro Regional de Bajío, Instituto de Ecología, Pátzcuaro, Michoacán, Mexico
INIFAP, Instituto Nacional Investigaciones Forestales Agricolas y Pecuarias, Mexico
LL, TEX, Lundell Herbarium, and herbarium of the University of Texas, Austin, TX, USA
MEXU, Herbario Nacional, Departamento de Botánica, Instituto de Biología, Universidad Autónoma de México, Mexico City, Mexico
MO, Missouri Botanical Garden Herbarium, St. Louis, MO, USA
NY, New York Botanical Garden Herbarium, Bronx, NY, USA
NRSP-6, National Research Support Program-6, Sturgeon Bay, WI, USA (formerly called the Inter-Regional Potato Introduction Project [IR-1])
PTIS, U.S. Potato Introduction Station Herbarium, Sturgeon Bay, WI, USA
US, United States National Museum, Smithsonian Institution, Washington, D.C., USA
WAG, Wageningen Agricultural University Herbarium, The Netherlands
WIS, University of Wisconsin Herbarium, Madison, WI, USA

TABLE 1.—*Summary of herbarium and germplasm records from NRSP-6 (the number in parentheses is the germplasm holdings) of Mexican wild potatoes before and after the 1997 expedition to Mexico. Prior germplasm records are listed in Roman type; new germplasm and herbarium collections are listed in* ***Bold Italic*** *type. Some states have herbarium records as determined in Materials and Methods but no germplasm records (listed as 0 below). New true seed collections followed by S, new tuber or in-vitro collections are followed by V, and new collections only as herbarium are followed by H. The germplasm collections still being increased at INIFAP are followed by an asterisk, while the others are already at NRSP-6. All collections are followed by the collection numbers. Because of ambiguity in identifications, the prior germplasm collections are listed as they appear in Bamberg et al. (1996), but our new collections appear by our working hypotheses of species boundaries (see text and Figure 2). Some collections are still at INIFAP or in U.S. quarantine and are here assumed to be increased eventually as true seed or as tubers at NRSP-6.*

Species	[1]States
Solanum agrimonifolium	CHIA (6, ***3S [959, 960, 961], 1H [963]***)
S. brachistotrichum	AGU (11, ***1H [910]***), CHIH (5, ***1V [923]***), DUR (2), JAL (1), SON (0), ZAC (4, ***1V [913]****),
S. brachycarpum	AGU (0, ***1H [906]***), GUE (0, ***3S [965, 966, 967]***), HID (4, ***2S [941, 943]***), JAL (3), MEX (10, ***2S [976, 982], 1H [942]***), MIC (6, ***3S [987, 988, 989], 1H [986]***), MOR (0), OAX (8, ***1S [958]***), PUE (2, ***1S [950]***), QUE (0), SIN (0), TLA (0), VER (1)
S. bulbocastanum subsp. *bulbocastanum*	CHIA (0), D.F. (11), GUE (1), HID (1), JAL (0), MEX (7), MIC (3), MOR (2), NAY (0), OAX (9, ***1V [956]****), PUE (3), QUE (0), TLA (1), VER (1)
S. bulbocastanum subsp. *dolichophyllum*	GUE (0), JAL (3), MEX (1), MIC (1), MOR (2), OAX (0)
S. bulbocastanum subsp. *partitum*	CHIA (1)
S. clarum	CHIA (1, ***1S [962]***)
S. cardiophyllum subsp. *cardiophyllum*	AGU ***[1V, 912*]***, D.F. (0), GUE (0), HID (2), JAL (1), MEX (0), MIC (0), MOR (0), OAX (1), PUE (5), QUE (1), ZAC (1, ***1H [914]***), UNK (6)
S. cardiophyllum subsp. *ehrenbergii*	AGU (1), D.F. (0), GUA (3, ***1V [993*]***), HID (0), JAL (8), MEX (0), MIC (0, ***1H [902]***), OAX (0), PUE (0), QUE (6), SLP (4), ZAC (8)
S. cardiophyllum subsp. *lanceolatum*	GUE (1), HID (1), OAX (0), PUE (1), TLA (0)
S. demissum	AGU (0, ***1S [909]***), CHIH (2), D.F. (23), DUR (2, ***1S [920]***), HID (6, ***1S [940]***), MEX (50, ***8S [971, 972, 975, 977, 984, 996, 997, 998]***), MIC (10), MOR (3), OAX (1), PUE (2), SLP (0), SIN (0), TLA (8), VER (2), UNK (19)
S. x *edinense* subsp. *edinense* and subsp. *salamanii*	D.F. (0), HID (0), MEX (1, ***8V [969, 970, 974, 980, 981, 983, 994, 995]***), MIC (0), OAX (0), TLA (0), VER (0)
S. fendleri subsp. *arizonicum* and subsp. *fendleri*	BC (3), CHIH (18), SON (0)
S. guerreroense	GUE (1), JAL (1), MEX (0)
S. hjertingii subsp. *hjertingii* and subsp. *physaloides*	COA (10, ***1V [927*]***), NL (1, ***1V [933*]***), SIN (0), TAM (0)
S. hintonii	MEX (0, ***1V [968*]***)
S. hougasii	GUE (0), JAL (6), MEX (0), MIC (5)
S. iopetalum	JAL (2), MEX (2), MIC (5), PUE (2), VER (0)
S. jamesii	CHIH (0), SON (0)
S. lesteri	OAX (3, ***1S [957]***)
S. leptosepalum	CHIH (0), COA (0, ***1S [926]***), NL (0)
S. macropilosum	NL (0, ***2S [931, 932]; 2V [928*, 930*]; 1H [929]***)
S. matehualae	PUE (0), SLP (2)
S. x *michoacanum*	MIC (1, ***1V [903*]***)
S. morelliforme	CHIA (4), GUE (2), MEX (2), MIC (2), OAX ***[1S, 954]***, PUE (3), VER (***1S [946], 1H 948]***)
S. nayaritense	JAL (1), MIC (0), NAY (2), ZAC (1)
S. oxycarpum	HID (0, ***1S [944]***), OAX (1, ***2S [952, 953]***), PUE (2, ***1S [951]***), QUE (0), VER (8, ***1S [949]***)
S. polyadenium	HID (2), JAL (2), MEX (0), MIC (13, ***1S 901]***) OAX (0, ***1H [955]***), PUE (1), VER (1)
S. polytrichon	AGU (2), CHIH (0), COA (0), DUR (2, ***1S [921]***), GUA (0), JAL (11), MIC (2), NAY (0), NL (0), PUE (0), QUE (12), SLP (1), ZAC (14, ***1S [915]***)
S. pinnatisectum	GUA (8), JAL (5), MIC (1), QUE (4), ZAC (0), UNK (1)
S. papita	CHIH (1), DUR (20), SON (0), ZAC (7)
S. x *sambucinum*	GUA (0, ***1V [992*]***), QUE (1)
S. schenckii	HID (0), OAX (3, ***1S [964]***), PUE (5), QUE (3), VER (0)
S. x *semidemissum*	D.F. (0), HID (0), MEX (0, ***1V [973]***), MOR (0), PUE (0), TLA (0)
S. stenophyllidium	JAL (1, ***1V [905*], 1H [904]***), ZAC (0)
S. stoloniferum subsp. *moreliae* and subsp. *stoloniferum*	AGU (0, ***1H [911*]***), CHIH (2), COA (0, ***1H [925]***), D.F. (3), DUR (1, ***1V [917*], 2H [918, 919]***), GUA (3), HID (16), JAL (2), MEX (38, ***1S [936]***), MIC (17), MOR (0), NL (0), OAX (10), PUE (5), QUE (10), SLP (0), TLA (6), VER (1), ZAC (0), UNK (10)
S. tarnii	HID (9), QUE (1), VER (1)
S. trifidum	JAL (6, ***1V [991*]***), MIC (7, ***1V [985*]***), UNK (1)
S. tuberosum	Only 1997 collections listed here. MEX(***[5V 969B, 978, 979, 999, 1000]***)
S. verrucosum	COA (1), COL (0), D.F. (1), GUA (0), HID (2, ***1S [939]***), JAL (8, ***1V [990*]***), MEX (7, ***1V [937]***), MIC (8), MOR (0), NL (6, ***1S [934], 1H [935]***), OAX (1), PUE (1), QUE (1), SLP (0), TAM (0), TLA (1), VER (0, ***1V [947*]***), UNK (2)
S. x *villuspetalum*	D.F. (0), MEX (0)

[1]AGU, Aguascalientes; BC, Baja California; CHIA, Chiapas; CHIH, Chihuahua; COA, Coahuila; COL, Colima; DUR, Durango; GUA, Guanajuato; GUE, Guerrero; HID, Hidalgo; JAL, Jalisco; MEX, Mexico; MIC, Michoacán; MOR, Morelos; NAY, Nayarit; NL, Nuevo León; OAX, Oaxaca; PUE, Puebla; QUE, Querétaro; SLP, San Luis Potosí; SIN, Sinaloa; SON, Sonora; TAM, Tamaulipas; TLA, Tlaxcala; UNK, locality unknown; VER, Veracruz; ZAC, Zacatecas.

ern Chile. It consists of seven cultivated and 225 wild species, according to the latest comprehensive taxonomic treatment of Hawkes (1990). Nine of these species are members of separate clades and are alternatively treated in sect. *Etuberosum* (Buk. and Kameraz) A. Child, sect. *Lycopersicum* (Mill.) Wettst., or sect. *Juglandifolium* (Rydb.) A. Child (Child 1990; Spooner *et al.* 1993).

Most wild potato species grow in the Andes, but 31 species and five hybrid species grow in Mexico (Table 1; Figure 1). Even though Mexico represented a well-collected region for potato germplasm, some species remained little-known or under-collected. For example, *S. hjertingii* var. *physaloides*, *S. leptosepalum*, and *S. macropilosum* were only known from a single collection each of herbarium specimens from their type localities. Other species were known from additional herbarium collections, but had no or few germplasm collections, such as *S. clarum*, *S.* x *edinense*, *S. hintonii*, *S. jamesii*, *S. lesteri*, *S.* x *michoacanum*, *S.* x *sambucinum*, and *S. stenophyllidium*. Other species had unresolved taxonomic problems that needed clarification by additional collections. Therefore, INIFAP, NRSP-6, IPK, and Wageningen Agricultural University identified Mexico as a high-priority area for collecting because of these missing germplasm accessions and taxonomic difficulties.

This report details the results of a germplasm collecting expedition in Mexico by these four institutions from August 21 to October 31, 1997. The goals of the expedition were to collect potato germplasm, to increase it quickly and to make

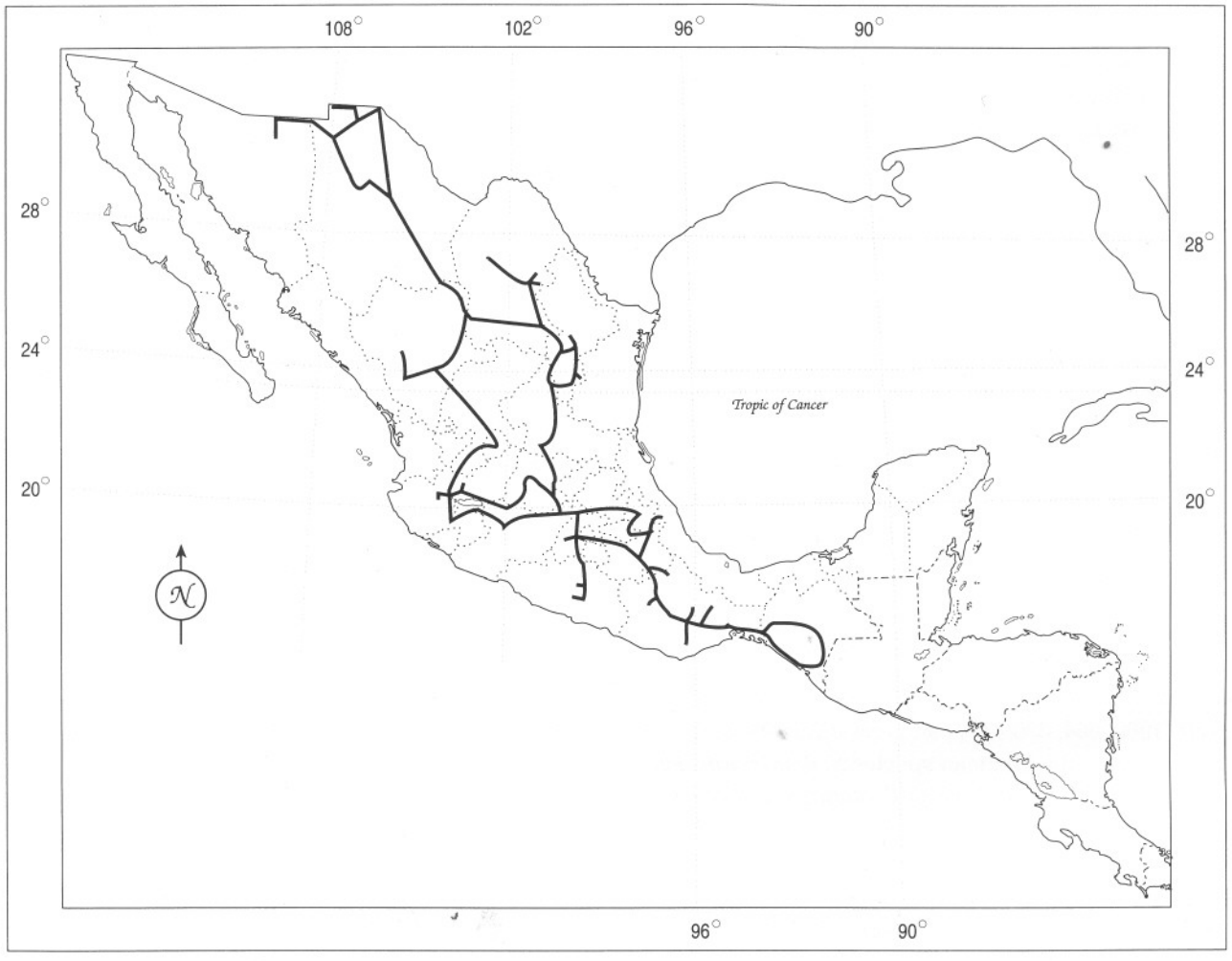

FIGURE 1.
Generalized map of collecting routes, Mexico, 1997.

it freely available internationally, and to gather field data for our taxonomic studies of these species.

Previous Potato Collecting in Mexico

Wild potato (*Solanum* sect. *Petota*) germplasm has been collected in Mexico on nine major expeditions, as determined by 20 collections or more from each expedition currently at the United States potato genebank, the National Research Support Program-6 (NRSP-6). These expeditions were conducted by D. Correll from 1947-1948, resulting in 64 currently surviving collections, J.G. Hawkes (1949, 26), K.M. Graham, (1953-1957, 43), J.G. Hawkes, J.P. Hjerting, and R.M. Lester (1958-1959, 103), T.R. Tarn (1967, 36), C.M. Ochoa and A. Rivera-Peña (1980, 24), T.R. Tarn, A. Rivera-Peña, J.P. Hjerting, R.W. Ross, J. Gómez (1982-1984, 187), D.M. Spooner, J.P. Hjerting, J. Gómez, A. Rodríguez, F. Flores (1988, 89), A. Rodríguez, O. Vargas, E. Villegas (1993, 37 germplasm collections, some still in quarantine). These and prior collections in Mexico are detailed in Rydberg (1924), Bukasov (1930), Hawkes (1941, 1944, 1959, 1966), Correll (1948a,b, 1952, 1962), Graham and Dionne (1961), Flores-Crespo, (1966), Ugent (1967, 1968), Tarn (1969), Ochoa and Schmiediche (1987), Spooner *et al.* (1991), Rivera-Peña and Molina-Galan (1989), Rodríguez and Vargas (1994), and Rodríguez *et al.* (1995).

Taxonomy of Mexican Wild Potatoes

The latest comprehensive taxonomic treatment of sect. *Petota* (Hawkes 1990) recognized 31 species and five hybrids occurring in Mexico (Table 1). Many of these species are morphologically very similar and difficult to identify. This similarity of Mexican species traditionally has led to great problems in distinguishing the species. It has resulted in different taxonomic treatments relative to numbers of species and hypotheses of affiliations of species to series (Spooner and Sytsma 1992; Spooner *et al.* 1995).

The difficulty to identify similar species even crosses traditionally recognized series boundaries. For example, Correll (1962: 364, 380-382) had great difficulty in distinguishing among the Mexican species *S. demissum* (ser. *Demissa*), *S. fendleri* (ser. *Longipedicellata*), *S. stoloniferum* (ser. *Longipedicellata*), and *S. verrucosum* (ser. *Tuberosa*) with vegetative characters, and relied on corolla shape to make final identifications. However, the differences in corolla shapes never have been quantified, and in actual practice, we found less than 10% of herbarium specimens have corollas, or if they have them, to be pressed adequately flat to clearly determine shape. As a result, many identifications are problematical. The taxonomic difficulty of Mexican wild potatoes is not unique to this region, as species also are difficult to identify and to classify in South America (Spooner and van den Berg 1992; van den Berg *et al.* 1998; Miller and Spooner 1999).

Solanum brachycarpum complex (S. brachycarpum, S. guerreroense, S. hougasii, and *S. iopetalum)*

These four species belong to *Solanum* series *Demissa*. As circumscribed by Hawkes (1990), series *Demissa* contains six hexaploid ($2n = 6x = 72$) species (additionally containing *S. demissum* and *S. schenckii*). In addition, Hawkes (1990) placed in this series three pentaploid ($2n = 5x = 60$) putative hybrid taxa (*S.* x *edinense* subsp. *edinense*, *S.* x *edinense* subsp. *salamanii*, *S.* x *semidemissum*). Series *Demissa* has been the subject of much disagreement regarding the assignment of species to series (Spooner and Sytsma 1992; Spooner *et al.* 1995). For example, species placed by Hawkes (1990) in series *Demissa* also have been placed in series *Conicibaccata* or series *Tuberosa* by Rydberg (1924), Hawkes (1944), Correll (1952, 1962), and Flores-Crespo (1966).

Spooner *et al.* (1995) studied the morphology of all six non-hybrid taxa in ser. *Demissa*, and of the morphologically similar species *S. albicans* (ser. *Acaulia*) and *S. verrucosum* (ser. *Tuberosa*). They showed that *S. demissum* was more similar to *S. albicans* than to all other species in ser. *Demissa*, and suggested that *S. demissum* may be related to members of ser. *Acaulia* (confined to South America), and not to other members of ser. *Demissa*. Subsequent morphological studies using more accessions of *S. albicans* and *S. acaule* (ser. *Acaulia*) by Kardolus (1999) also supported the relationship of *S. demissum* to members of ser. *Acaulia*. Further, Kardolus and Groendijk-Wilders (1998) showed that *S. demissum* shared a similar inflorescence architecture with ser. *Acaulia*. This relationship also has been supported by molecular data from single- to low-copy nuclear restriction fragment length polymorphisms (RFLPs; Debener *et al.* 1990), chemical data from steroidal glycoalkaloids (Petersen *et al.* 1993), and cladistic (but not phenetic) analysis of Amplified Fragment Length Polymorphisms (AFLPs) (Kardolus 1998).

Spooner *et al.* (1995) also showed that *S. guerreroense*, *S. iopetalum*, and *S. hougasii* were difficult to consistently distinguish from *S. brachycarpum*. They showed that the characters defining species were extremely variable and not species-specific, and that species could be distinguished only

by reliance on a range of character states that were shared by other species. They concluded that the species of ser. *Demissa* needed reevaluation, and that a determination of the validity of *S. guerreroense*, *S. hougasii*, and *S. iopetalum* needed data from additional collections.

Solanum stoloniferum complex (S. fendleri, S. papita, S. stoloniferum)

Similar to the hexaploid species of *Solanum* series *Demissa*, the tetraploid species of series *Longipedicellata* are morphologically very similar and difficult to distinguish. Hawkes (1990) recognized six species and one hybrid species in this series (Table 1). Morphological data of Spooner, van den Berg, and Miller (in press) indicated that three of these species, *Solanum fendleri*, *S. papita*, and *S. stoloniferum* are so similar as to perhaps represent a single species. Although not part of this complex, these unpublished data also suggest that two other members of ser. *Longipedicellata*, *S. hjertingii* and *S. matehualae*, are the same species.

Solanum macropilosum

Prior to this expedition, *S. macropilosum* was known from a single collection at Cerro El Viejo, in the state of Nuevo León. Correll (1961) described this single collection as a new species because of its leaves with three leaflets with an enlarged terminal leaflet, and long, coarse shaggy hairs. He indicated that it superficially resembled *S. wightianum* Rydb., a tetraploid Mexican species synonymized by Hawkes (1990) under *S. polytrichon* Rydb. in the series *Longipedicellata*. Correll also indicated *S. macropilosum* resembled *S. flahaultii* Bitter, a tetraploid Colombian species later placed by Hawkes (1990) in the series *Conicibaccata*. Correll (1962) placed *S. macropilosum*, *S. wightianum*, and *S. leptosepalum* as the only three representatives of the Mexican series *Borealia* Correll, characterized by leaves typically with three leaflets and a rotate corolla.

Hawkes (1990) tentatively placed *S. macropilosum* in series *Tuberosa*. He noted a similarity of it to *S. verrucosum*, but with a less dissected leaf (1-2 jugate) with large terminals and no interjected leaflets, corollas without the characteristic lobes typical of *S. verrucosum*, and a denser, longer pubescence on stems and inflorescence branches.

Solanum leptosepalum

Like *S. macropilosum*, *S. leptosepalum* was known from a single herbarium collection, at the Sierra de la Gloria in the state of Coahuila. It was similar to *S. macropilosum* regarding its three leaflets with an enlarged terminal leaflet, and Correll (1962) placed this species in series *Borealia*. Hawkes (1990) tentatively placed this species in series *Tuberosa*, and noted a similarity of it to *S. verrucosum*, but with slightly longer calyx acumens and apparently non-verrucose fruits. He suggested that *S. leptosepalum* may possibly represent a subspecies of *S. verrucosum*.

Solanum agrimonifolium and S. oxycarpum

These two species are morphologically very similar and have been grouped by all authors in series *Conicibaccata* Bitter, a series characterized partly by conical fruits. They have been distinguished by Correll (1962) and Hawkes (1990) based mainly on numbers of lateral and interjected leaflets and fruit size. *Solanum agrimonifolium* has higher numbers of lateral and interjected leaflets and larger fruits than *S. oxycarpum*.

Solanum ser. *Conicibaccata* has diploids, tetraploids, and hexaploids, but germplasm identified as *S. agrimonifolium* and *S. oxycarpum* have all been determined to be tetraploid ($2n = 4x = 48$) (Correll 1962; Hawkes 1990; Bamberg *et al.* 1996), providing no aid in separating them. Correll (1962) and Hawkes (1990) identified Mexican collections from the northern-most distribution of the complex in the states of Puebla, Oaxaca, and Veracruz as *S. oxycarpum*, and collections more to the southeast in Chiapas State and adjacent Guatemala and Honduras as *S. agrimonifolium*.

It is farther to the south in Costa Rica that the alternative taxonomic treatments of *S. oxycarpum* occur. Correll (1962) identified all Costa Rican collections as *S. oxycarpum* (including *S. longiconicum*). Hawkes (1990) considered *S. oxycarpum* to be a species confined to Mexico. He distinguished *S. oxycarpum* from *S. longiconicum* (Costa Rica and Panama) by the former with glabrous leaves (no hairs), and the latter with subglabrous leaves (only slightly hairy). Because of these taxonomic ambiguities, we decided to collect *S. agrimonifolium* and *S. oxycarpum* throughout their range in Mexico, and to use these data for future studies on the boundaries of the Central American members of *Solanum* series *Conicibaccata*.

MATERIALS AND METHODS

This expedition was initiated by a collecting request by the USDA, Agricultural Research Service to INIFAP, who secured permission to collect from the Mexican Department of State. Prior or during the expedition, we compiled locality

data from (1) a database backing up germplasm records from NRSP-6 (Bamberg *et al.* 1996); (2) a database of locality records we obtained from examination of herbarium sheets at the following herbaria (herbarium codes follow Holmgren *et al.* [1990] and are listed above under Explanation of Abbreviations): CHAP, CHAPA, ENCB, F, GH, IEB, LL, TEX, MEXU, MO, NY, PTIS, US, WAG, WIS; and (3) a database of locality records from Hawkes (1997). The herbarium PTIS will appear in the next edition of Holmgren *et al.* (1990), but is now introduced in Bamberg and Spooner (1994).

We merged these three files into a single database and established a common format. We placed a first priority on collecting those species with no or few collections, and a second priority on obtaining records from states with herbarium records but no germplasm samples. Additionally, we collected herbarium samples from some previously known sites of *S. agrimonifolium* and *S. oxycarpum* to help resolve their taxonomic status.

We determined localities with the aid of (1) United States Department of the Interior (1956), (2) the 1:250,000-scale topographic maps (121 sheets) from the Instituto Geográfico Militar, (3) Instituto Nacional de Estadística, Geografía e Informática (1997), (4) Roji-García and Roji-García (1997). Longitude and latitude data were obtained by a global positioning system and altitudes with an altimeter.

New collections are listed in Table 1. Herbarium vouchers are deposited at MEXU, PTIS, WAG, and at the INIFAP station in Toluca. Collections from September 2 to September 25 are labeled *RSS* (*Rivera-Peña*, *Spooner*, and *Schüler 901-935*), while those from September 30 to October 27 are *RSV* (*Rivera-Peña*, *Spooner*, and *van den Berg*) *936-1000*. True seeds were preferentially collected as germplasm samples to avoid the added expenses of screening and eliminating tuber-borne diseases, except for the putative hybrid taxon *S.* x *edinense* and landrace cultivars of *S. tuberosum*. When true seeds were not available, we collected germplasm as tubers or plants in pots. Some germplasm collections were divided between INIFAP and NRSP-6, while those collected in low numbers or as vegetative collections were left at INIFAP for a germplasm increase. A second increase will be performed by NRSP-6, with later free distribution internationally.

RESULTS AND DISCUSSION

New Germplasm Collections

We collected along the route shown in Figure 1, and made the first germplasm collections of *S. hjertingii* var. *physaloides*, *S. leptosepalum*, *S. macropilosum*, and *S.* x *sambucinum* (Table 1). Also, germplasm collections were made of *S.* x *edinense* (one germplasm collection before, now eight more), *S.* x *michoacanum* (one, now two), *S. stenophyllidium* (one, now two). In addition, we have gathered morphological data in the field of species groups that are in need of taxonomic resolution: (*S. agrimonifolium* and *S. oxycarpum*), the *S. brachycarpum* complex, and the *S. stoloniferum* complex.

Our collections in 1997 were wide-ranging throughout much of Mexico in order to meet our germplasm and taxonomic collecting goals as discussed above. Much of the northern portion of Mexico (north of the Mexican transvolcanic belt) was experiencing a drought in 1997 and our success in collecting germplasm as true seed was much greater in the south that had adequate rainfall for most wild potato populations to produce fruits.

Complete passport data of the germplasm collections can be obtained from the authors or from NRSP-6, where all germplasm collections have been entered into the Germplasm Resources Information Network (GRIN). These data eventually will be published in a taxonomic treatment of the potatoes of North America, in preparation by Spooner and collaborators.

Taxonomy

Solanum stoloniferum Complex—We made six collections of this complex (*RSS 911, 925, 917, 918, 919, RSV 936*; in our expanded sense to also include *S. fendleri* and *S. papita*). We presently are using our collections, and others at NRSP-6, to test the diagnostic nature of morphological characters. We continue to be unable to distinguish *S. fendleri*, *S. papita*, and *S. stoloniferum* in the field, as the key characters separating the taxa from Correll (1962) and Hawkes (1990) appear to intergrade almost completely. Consequently, we identify all our collections of these three species by the earliest name, *S. stoloniferum*.

Solanum brachycarpum Complex—We made 15 collections of this complex (*RSS 906, RSV 941, 942, 943, 950, 958, 965, 966, 967, 976, 982, 986, 987, 988, 989*; in our expanded sense to also include *S. guerreroense*, *S. hougasii*, and *S. iopetalum*). We noted extensive variation in corolla color (purple to purple splashed with white) and fruit shape (spherical to conical) in our collections of this complex. Most collections had corollas colored purple and had fruits that varied greatly in shape from ovoid to conical and with smooth surfaces. Collections *RSV 966* and *967* had corollas

purple streaked with white and conical fruits with smooth surfaces. Collections *RSV 987, 988, 989* were most distinctive with corollas purple streaked with white and with globose verrucose fruits, and may represent *S. hougasii*. The lack of clear character states separating these taxa makes identifications difficult, and we presently identify all of our collections by the earliest name, *S. brachycarpum*.

Solanum agrimonifolium and S. oxycarpum—Before collecting, our herbarium work documented an additional state record of *S. agrimonifolium* or *S. oxycarpum* in the area of Puebla, Oaxaca, and Veracruz, where Correll (1962) and Hawkes (1990) recognize *S. oxycarpum* to grow: Hidalgo: 20 km E of Metepec, Municipio Metepec, *Hernandez and Hernandez 4772* (ENCB, MEXU). We collected this species there (*RSV 944*), and in Veracruz (*RSV 949*), Puebla (*RSV 951*), and Oaxaca (*RSV 952, 953*). In addition, we collected in Chiapas State where *S. agrimonifolium* is recognized to grow (*RSV 959, 960, 961, 963*).

Like Correll (1962) and Hawkes (1990), our collections documented most specimens from the "*S. oxycarpum* area" to generally have fewer lateral and interjected leaflets than from specimens more to the southwest at Chiapas. An exception was collection *RSV 944*, which had many lateral and interjected leaflets like *S. agrimonifolium*. However, it was easy to find exceptions within populations that showed numbers to cross traditional species boundaries. We here conservatively maintain identifications as *S. agrimonifolium* and *S. oxycarpum* as based on the geographical criteria mentioned previously until we analyze the morphological and molecular characters of more collections from throughout Mexico and Central America.

Solanum leptosepalum—The type locality of *S. leptosepalum* simply indicates "Sierra La Gloria southeast of Monclova." The Sierra La Gloria is a distinct isolated mountain range just southeast of Monclova running northwest to southeast, and about 40 km long and 15 km wide, with the upper elevation at 2180 m. We first searched on the southwest side of the mountains, in an area of dry vegetation. We located the species (*RSS 926*) another time, however, on the top of the mountain, ascending from the northeast side of the mountain, through mesic vegetation. We ascended much of the mountain on a private dirt road, beginning from a point about 15 km east of Monclova. The species was very low growing and nestled among rocks at the top of the mountain, and had three to five leaflets with the terminal leaflet enlarged and with globose fruits. The species appears to us to be a member of the *S. stoloniferum* complex, not like *S. verrucosum* (see Introduction). We await further determinations of chromosome number, observations of plants in the greenhouse, and molecular results before we make a determination on species boundaries and affiliations.

Solanum macropilosum—We made two collections that we provisionally identify as *S. macropilosum* at Cerro El Viejo, hiking east-northeast into the mountains from the town square of Zaragoza (*RSS 931, 932*). We also made three other collections nearby that appear similar (*RSS 928, 929, 930*). These collections have strongly verrucose ovoid fruits, and some of the plants have an enlarged terminal leaflet like the type of *S. macropilosum*. The collections appear to us to be typical of *S. verrucosum* (Spooner *et al.* 1995). Like with *S. leptosepalum* (above), these await further determinations of chromosome number, observations of plants in the greenhouse, and molecular results before we make a determination on species boundaries and affiliations.

Taxonomy Summary

We summarize our tentative taxonomic conclusions regarding species boundaries in Figure 2. This represents our working hypotheses of species boundaries in order to identify our collections, and is *not* intended to serve as a formal synonymy of these species. We await more detailed morphological and molecular studies of our collections before we make final taxonomic decisions.

Germplasm Distribution

Seed and some tuber collections from the expedition were divided between INIFAP and NRSP-6. Living plant and some tuber collections were left at INIFAP for increases as true seed or tuber collections, with the first increase to be divided between INIFAP and NRSP-6. The second increase at NRSP-6 will be made freely available internationally. Herbarium specimens are deposited at INIFAP, MEXU, PTIS, and WAG.

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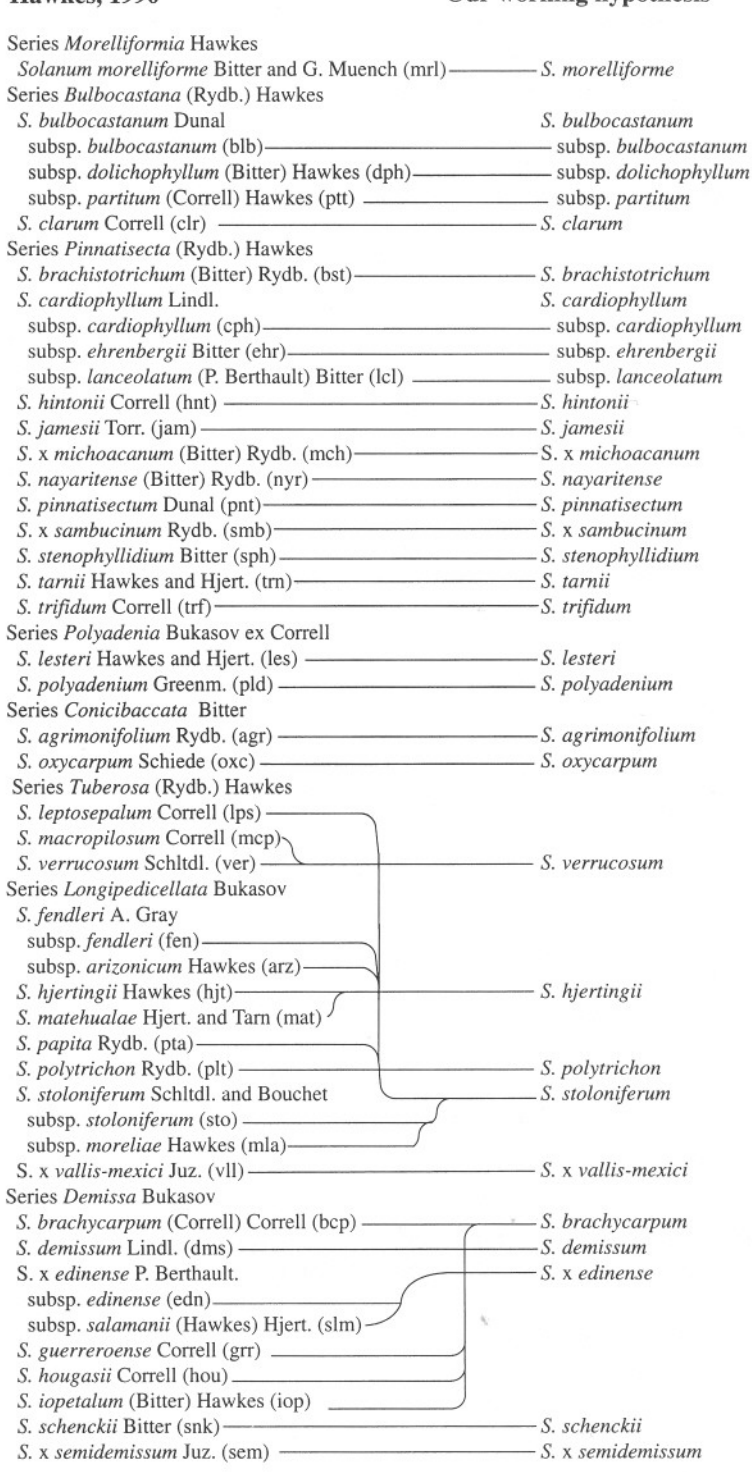

FIGURE 2.
Alternative hypotheses of species in Mexico by Hawkes (1990) and by us. Because of ambiguity of series affiliations we do not group species in series. Our taxonomic decisions are preliminary and are not intended to constitute a formal synonymy. Three-letter species codes follow Hawkes (1990) and correspond to codes in Table 1.

ment group headquartered in Monterrey, Mexico; the Institut für Pflanzengenetik und Kulturpflanzenforschung Gatersleben; Gemeinschaft zur Förderung der Kulturpflanzenforschung Gatersleben e. V.; Wageningen Agricultural University; and the Netherlands Organization for Scientific Research (NWO). We also thank John Bamberg and staff of NRSP-6 for growing the accessions after import into the United States, Aarón Rodríguez and two anonymous reviewers for review of the manuscript, and Dr. Jorge Alberto Cárdenas de los Santos for allowing us access to his land and accompanying us to the type locality of *S. leptosepalum*.

LITERATURE CITED

Bamberg, J.B., M.W. Martin, J. Schartner, and D.M. Spooner. 1996. Inventory of tuber-bearing *Solanum* species. Potato Introduction Station, NRSP-6, Sturgeon Bay, WI.

Bamberg, J.B. and D.M. Spooner. 1994. The United States potato introduction station herbarium. Taxon 43:489-496.

Bukasov, S.M. 1930. The cultivated plants of Mexico, Guatemala and Colombia (in Russian, English summary). Trudy Prikl Bot Suppl 47:191-226, 513-525.

Child, A. 1990. A synopsis of *Solanum* subgenus *Potatoe* (G. Don) (D'Arcy) (*Tuberarium* (Dun.) Bitter (s.l.)). Feddes Repert 101:209-235.

Correll, D.S. 1948a. Collecting wild potatoes in Mexico. USDA Circ 797:1-40.

Correll, D.S. 1948b. Wild potato collecting in Mexico. Field and Lab 16:94-112.

Correll, D.S. 1952. Section *Tuberarium* of the genus *Solanum* of North America and Central America. USDA Agric Monogr 11:1-243.

Correll, D.S. 1961. New species and some nomenclatural changes in section *Tuberarium* of *Solanum*. Wrightia 2:169-197.

Correll, D.S. 1962. The potato and its wild relatives. Contrib Texas Res Found Bot Stud 4:1-606.

Debener, T., F. Salamini, and C. Gebhardt. 1990. Phylogeny of wild and cultivated *Solanum* species based on nuclear restriction fragment length polymorphisms (RFLPs). Theor Appl Genet 79:360-368.

Flores-Crespo, R. 1966. Estudio preliminar del genero *Solanum*, seccion *Tuberarium* subseccion *Hyperbasarthrum* en México. Tesis, Univ Nac Autonoma de México, México, D.F.

Graham, K.M. and L.A. Dionne. 1961. Crossability relationships of certain diploid Mexican *Solanum* species. Canad J Genet Cytol 3:121-127.

Hawkes, J.G. 1941. Potato collecting expeditions in Mexico and South America. Imp Bur Pl Breed Genet, Imp Agric Bur, Cambridge. pp. 1-30.

Hawkes, J.G. 1944. Potato collecting expeditions in Mexico and South America. II. Systematic classification of the collections. Imp Bur Pl Breed Genet, Imp Agric Bur, Cambridge. pp. 1-142.

Hawkes, J.G. 1959. The Birmingham University plant collecting expedition to Mexico and Central America. Univ Birmingham Gaz 11:60-63.

Hawkes, J.G. 1966. Modern taxonomic work on the *Solanum* species of Mexico and adjacent countries. Am Potato J 43:81-103.

Hawkes, J.G. 1990. The potato: evolution, biodiversity and genetic resources. Belhaven Press, Oxford.

Hawkes, J.G. 1997. A database for wild and cultivated potatoes. Euphytica 93:155-161.

Holmgren, P.K., N.H. Holmgren, and L.C. Barrett. 1990. Index herbariorum, Part I: the herbaria of the world. Ed. 8. Regnum Veg 120:1-693.

Instituto Nacional de Estadística, Geografía e Informática. 1997. Estados Unidos Mexicanos, Conteo de poblacion y vivienda, resultados definitivos. Instituto Nacional de Estadística, Geografía e Informática INEGI), Aguascalientes, Mexico.

Kardolus, J.P. 1998. A biosystematic study of *Solanum acaule*. Thesis, Wageningen Agricultural University, The Netherlands.

Kardolus, J.P. 1999. Morphological variation within series *Acaulia* Juz. (*Solanum* sect. *Petota*). *In*: Nee, M., and D.E. Symon (eds). Solanaceae IV. Royal Botanic Gardens, Kew.

Kardolus, J.P. and N. Groendijk-Wilders. 1998. The inflorescence architecture of *Solanum acaule* and related taxa of *Solanum* section *Petota* (Solanaceae). Acta Bot Neerl 47:195-207.

Miller J.T. and D.M. Spooner. 1999. Collapse of species boundaries in the wild potato *Solanum brevicaule* complex (Solanaceae, *S.* sect. *Petota*): molecular data. Plant Syst Evol 214:103-130.

Ochoa, C. and P. Schmiediche. 1987. Status of the collections at CIP: wild species. *In*: Strategies for the conservation of potato genetic resources IV. International Potato Center, Lima, Peru, pp. 19-26.

Petersen, H.W., P.A. Molgaard, U. Nyman, and C.E. Olsen. 1993. Chemotaxonomy of the tuber-bearing *Solanum* species, subsection *Potatoe* (Solanaceae). Biochem Syst Ecol 21:629-644.

Rivera-Peña, A. and J. Molina-Galan. 1989. Wild tuber-bearing species of *Solanum* and incidence of *Phytophthora infestans* (Mont.) de Bary on the western slopes of the Nevado de Toluca 1. *Solanum* species. Potato Res 32:181-195.

Rodríguez, A. and O. Vargas-P. 1994. Las especies de papa silvestre (*Solanum* L. sección *Petota* Dumortier) en Jalisco. Boletín del Instituto de Botánica, IBUG 2:1-68.

Rodríguez, A., O. Vargas, E. Villegas, and D.M. Spooner. 1995. Wild potato (*Solanum* sect. *Petota*) germplasm collecting expedition to Mexico in 1993, with special reference to *Solanum bulbocastanum* Dunal and *S. cardiophyllum* Lindley. Potato Res 38:47-52.

Roji-García, A.P. and J.P. Roji-García. 1997. Gran atlas de carreteras, 1997-1998 (individual road maps for all 32 Mexican states and the Distrito Federal, with index for each state; scale varies from 1:140,000 [Distrito Federal] to 1:1,630,000 [Sonora]). Guia Roji S.A. de C.V. Distrito Federal, Mexico.

Rydberg, P.A. 1924. The section *Tuberarium* of the genus *Solanum* in Mexico and Central America. Bull Torrey Bot Club 51:145-154.

Spooner, D.M., G.J. Anderson, and R.K. Jansen. 1993. Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepinos (Solanaceae). Amer J Bot 80:676-688.

Spooner, D.M., J.B. Bamberg, J.P. Hjerting, and J. Gómez. 1991. Mexico 1988 potato germplasm collecting expedition and utility of the Mexican potato species. Am Potato J 68:29-43.

Spooner, D.M. and K.J. Sytsma. 1992. Examination of series relationships of Mexican and Central American wild potatoes (*Solanum* sect. *Petota*): evidence from chloroplast DNA restriction site variation. Syst Bot 17:432-448.

Spooner, D.M. and R.G. van den Berg. 1992. An analysis of recent taxonomic concepts of wild potatoes (*Solanum* sect. *Petota*). Genet Res Crop Evol 39:23-37.

Spooner, D.M., R.G. van den Berg, and J.B. Bamberg. 1995. Examination of species boundaries of *Solanum* series *Demissa* and potentially related species in series *Acaulia* and series *Tuberosa* (sect. *Petota*). Syst Bot 20:295-314.

Spooner, D.M., R.G. van den Berg, and J.T. Miller. In press. Species and series boundaries of *Solanum* series *Longipedicellata* and phenetically similar species in ser. *Demissa* and ser. *Tuberosa*: implications for a practical taxonomy of sect. *Petota*. American Journal of Botany.

Tarn, R. 1969. New collections of potato species from Mexico. Am Potato J 46:357-358.

Ugent, D. 1967. Morphological variation in *Solanum* x *edinense*, a hybrid of the common potato. Evolution 21:696-712.

Ugent, D. 1968. The potato in Mexico: geography and primitive culture. Econ Bot 22:108-123.

United States Department of Interior. 1956. Gazetteer of Mexico: official standard names approved by the U.S. Board on Geographic Names. Division of Geography, Department of Interior, U.S. Government, Washington, DC.

Van den Berg, R.G., J.T. Miller, M.L. Ugarte, J.P. Kardolus, J. Villand, J. Nienhuis, and D.M. Spooner. 1998. Collapse of species in the wild potato *Solanum brevicaule* complex (Solanaceae: sect. *Petota*). Amer J Bot 85:92-109.